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Nudibranch Predators of Octocorallia

By Eric Brown

A Capstone Review Paper

Submitted in Partial Fulfillment of the Requirements for the Degree of

Masters of Science:

Marine Biology

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Capstone Committee Approval

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Table of Contents

List of Figures	ii
List of Tables.....	ii

PART I. Nudibranch Corallivores of Octocorals

1.0	Introduction	1
2.0	Corallivory.....	2
3.0	Octocorallia	4
4.0	Molluscan Predators of Octocorals.....	6
4.1	Nudibranch Corallivores	6
4.2	Phylum Mollusca	7
4.3	Class Gastropoda	7
4.3.1	Clade Heterobranchia.....	9
4.3.2	Informal Group Opisthobranchia.....	9
4.3.3	Subclade Nudibranchia	9
4.3.4	Clade Euctenidiacea.....	10
4.3.5	Clade Dexiarchia	11
5.0	Morphology of Feeding Organs	13
6.0	Prey Selection.....	18
7.0	Comparisons of Feeding Structures.....	21
8.0	Feeding Strategies.....	26
9.0	Locating Prey.....	31

PART II. Distribution and density of the corallivorous nudibranch *Tritonia hamnerorum* on the sea fan *Gorgonia ventalina* in the Florida Keys, USA: Personal Observation and Field Work.....33

10.0	Introduction	33
11.0	Background	36
12.0	Materials and Methods.....	38
13.0	Data and Results	39
14.0	Conclusion and Discussion	41
15.0	Summary	42
16.0	Literature Cited.....	49

List of Figures

Figure 1: A. <i>Tritonia hamnerorum</i> on <i>Gorgonia ventalina</i> , B. <i>Tritonia pikensi</i>	4
Figure 2: Body plan of a holaxonian octocoral	5
Figure 3: Typical body plans of nudibranch subclades	11
Figure 4: Detail of the buccal mass structure of <i>Tritonia hombergi</i>	13
Figure 5: Radular morphology and jaws of <i>Armina juliana</i>	14
Figure 6: Illustration of radular teeth arrangement	14
Figure 7: Detail of animal and radular tooth of <i>S. gerberina</i> and <i>S. sakuracea</i>	15
Figure 8: <i>Onchidoris billamellata</i> . Sagittal section of the head during feeding cycle	17
Figure 9: Detail of oral cavity, inner lip, outer lip and jaws of <i>Armina maculata</i>	17
Figure 10: <i>Tritonia festiva</i> on <i>Lophogorgia chilensis</i>	20
Figure 11: <i>Marioniopsis fulvicola</i> on <i>Parerythropodium fulvum fulvum</i>	23
Figure 12: Radulas of octocoral, bryozoan and anemone predators	25
Figure 13: Diagram of Lymnaea feeding cycle	27
Figure 14: <i>Tritonia diomedea</i> attacking <i>Ptilosarcus gurneyi</i>	29
Figure 15: <i>Armina maculata</i>	30
Figure 16: <i>Tritonia hamnerorum</i>	34
Figure 17: <i>Tritonia hamnerorum</i> on <i>Gorgonia ventalina</i>	36
Figure 18: Area of observation in Key Largo, FL.....	39
Figure 19: <i>Tritonia hamnerorum</i> on <i>Gorgonia ventalina</i>	39
Figure 20: An outbreak of <i>Tritonia hamnerorum</i> on <i>Gorgonia ventalina</i>	44

List of Tables

Table 1: Summary of known dietary interactions of <i>Tritonia</i> species	19
Table 2: Some radular characteristics of nudibranchs consuming anthozoans.....	22
Table 3: Record of nudibranchs observed in Key Largo in 2009	40
Table 4: Selected nudibranchs and octocoral prey	47

Introduction

Nudibranchs are soft-bodied marine heterobranch gastropod molluscs which lack a shell and mantle cavity. The basic body plan is bilaterally symmetrical with an expanded notum (the dorsal surface of the mantle), but in regards to other physical characteristics they exhibit a wide range of forms. Compared to other molluscs, evolutionarily the head and body became flattened and streamlined and tentacles have been lost or shifted to different areas of the body. Nudibranchs are found in many variations of size and color; despite the fact that these animals in general are noted for flamboyant colors and prominent external anatomical structures, many species rely upon a more cryptic appearance in order to remain inconspicuous as a defense mechanism.

Nudibranch means “naked gill” since they possess dorsal external gills and branchial plumes. Consisting of over 3000 species, they are the largest clade of heterobranchs (Bouchet & Rocroi 2005) and are found in a wide variety of biogeographic regions. The almost exclusively carnivorous nudibranchs are one of the top predators of filter feeding organisms such as corals, hydroids, and sponges (Garcia 1990). With the loss of the shell came increasing development of chemical and biological defenses, and different dietary specializations emerged. As a result, these mostly benthic, soft-bodied animals became virtually immune to attacks by predators (Gosliner 1987).

This paper provides a comprehensive review of the nudibranchs that feed on octocorals (Cnidaria, Anthozoa) emphasizing their feeding physiology and strategies, including prey location and selection. In particular, the question of whether feeding mechanics and morphology are similar among nudibranch corallivores that prey on related octocorals is addressed. One way this paper will identify worldwide patterns in

nudibranch/octocoral relationships is through the investigation of co-evolution. For example, in the North Pacific, neighboring colonies of the encrusting soft coral *Discophyton rudyi* retract their polyps in response to chemical cues as they are preyed upon by *Tritonia festiva*, which attempts to neutralize this strategy by launching brief, rapid surprise attacks on its target (Goddard 2006). If correlations can be found between feeding structures and type of prey, it may be possible to predict the diet of nudibranchs with unknown prey.

The relationship between nudibranchs and their food is extremely important. Nudibranchs have a varied diet of mostly toxic and chemically well-defended prey including corals, hydroids, sponges, and other nudibranchs (McDonald 1999). Having lost the protective shells possessed by closely related species, nudibranchs have replaced them with a variety of alternate defenses (Slattery 1998), including toxic chemical deterrents sequestered from their cnidarian prey, and cryptic coloration designed to mimic the substrate on which they reside. For example, *Phyllodesmium jakobsenae* resembles its *Xenia* prey, and *Phyllodesmium briareum* has external organs (cerata) that resemble its *Briareum* prey (Wägele 2005). Alternatively, many species advertise their toxicity with vivid colors, making them some of the most striking creatures in the ocean.

Corallivory

Corallivory is the consumption of live coral tissue by predators and grazers. With increases in other threats to coral reef ecosystems (e.g., climate change, disease, and eutrophication), corallivory may be important in reducing benthic cover; however, this factor is often overlooked and poorly understood. Still, when large numbers of

corallivores appear on a reef, their impacts are immediate and may be catastrophic. In 1970, the Crown of Thorns starfish, *Acanthaster planci*, devastated reefs in the Pacific (Porter 1972). A 1994 infestation of the corallivorous mollusc *Drupella cornus* (Muricidae, Rapaninae) was responsible for a >75% reduction of coral on Ningaloo reef in Western Australia (Black & Johnson 1994). Although nudibranchs do not cause mass destruction of corals as do *Acanthaster* and *Drupella* in the Indo-Pacific, they can affect growth, reproduction and survival in important ways. A coral colony need not be completely consumed by the corallivore to be negatively affected; scars created by grazing predators may lower the defenses of the coral, making it susceptible to infection from disease and colonization of its vacant skeleton by other organisms such as filamentous algae (Cronin *et al.* 1995). Repairing damage wastes valuable resources and reduces growth efficiency (Hayes 1990a). Additionally, physical damage to the coral can reduce gonadal biomass, severely reducing reproductive output and making it difficult for affected populations to recover (Linares *et al.* 2007). Tsounis (2006) found evidence of lower fertility in smaller colonies of the Mediterranean red gorgonian *Corallium rubrum*.

Stony Corals (Scleractinia) employ a variety of defenses against predators, such as stinging nematocysts, sweeper tentacles, and allelochemicals (Hayes 1990b). Although lacking sweeper tentacles, soft corals (Octocorallia, Alcyonacea) also have nematocysts and allelochemicals, and add other protective mechanisms such as carbonate sclerites that provide a structural deterrent, and anti-fungal, anti-bacterial, and anti-fouling compounds (Dube *et al.* 2002). However, organisms that consume corals have found ways to circumvent, and in some cases, exploit these defenses. Figure 1 shows some examples of nudibranch corallivory.



a.

b.

Fig. (1) a. *Tritonia hamnerorum* on *Gorgonia ventalina*, Key Largo, FL (Photo by Joshua Feingold), b.

Tritonia pikensi www.seaslugforum.net (Photo by A. Clark).

Octocorallia

Octocorallia, also known as Alcyonaria, are conspicuous and plentiful on the world's reefs. Each polyp in a colony has eight pinnate tentacles (Fig. 2). Included in this subclass are 3 subgroups: Alcyonacea, Pennatulacea and Helioporacea; each of these is taken into consideration in this review. Commonly known as soft corals, sea rods, sea fans, sea whips, sea pens and sea plumes, octocoral colonies take on a variety of different branching patterns and are anchored in place by a single holdfast. Helioporacea includes 2 families of blue corals which possess an aragonite skeleton. Order Pennatulacea includes 14 families of sea pens; the axial polyp has differentiated into a basal peduncle and a distal rachis to anchor into soft sediment. The third order, Alcyonacea, includes 28 families of soft corals and sea fans. These organisms are divided into two groups: the first

consists of soft corals with no skeletal axis: the groups Protalcyonaria, Stolonifera, and Alcyoniina. The second group includes sea fans with a skeletal axis which may consist of scleroproteinous gorgonin imbedded with CaCO_3 . They include the group Scleraxonia and the suborders Holaxonia and Calcaxonia (McFadden *et al* 2006). The central axis of the octocoral colony is surrounded by the coenenchyme in which the individual polyps are embedded; nudibranch corallivores may feed on both.

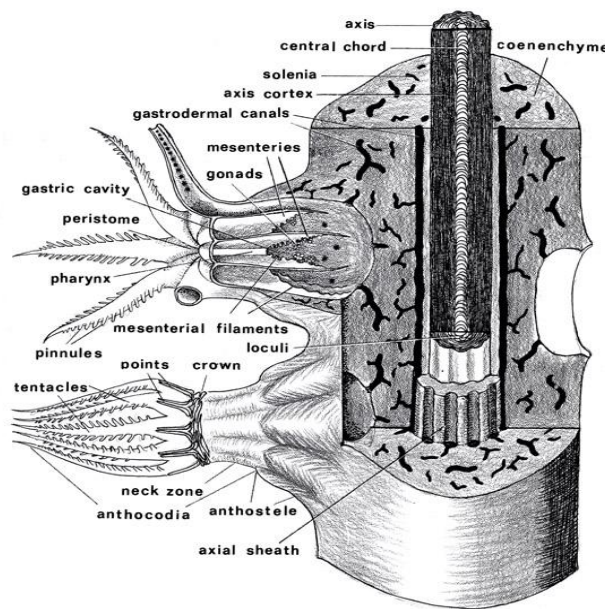


Fig. (2) Body plan of a holaxonian octocoral (from Bayer *et. al.* 1983).

Octocorals such as sea fans and sea whips (commonly called gorgonians), although not structural reef forming entities, nonetheless provide important habitat for a variety of reef-dwelling organisms. Additionally, octocorals may dominate benthic communities that attract recreational divers who help support local economies. Octocorals are rarely consumed by predators due to protection

by a variety of defense mechanisms and their low nutritional value, yet specialized predators may cause a great deal of damage to these valuable organisms.

Molluscan predators of octocorals

A variety of organisms feed on octocorals, including fish [*Alutera scripta* (Monacanthidae), *Chaetodon capistratus* (Chaetodontidae)] and the bristleworm *Hermodice carunculata* (Amphinomidae) (O’Neil and Pawlik 2002). Very few mollusc species, such as the nudibranch *Tritonia hamnerorum* (Fig 1.), and the Flamingo Tongue snail *Cyphoma gibbosum* (Ovulidae), specialize on octocorals.

Molluscs have a wide range of feeding specializations, including some bizarre and extraordinary adaptations. Molluscan corallivores use a variety of feeding mechanisms when feeding on octocorals, such as grazing on individual polyps or the tissue between them, with varying effect. Although this rarely kills the colony, because only portions of the colony are usually consumed and tissues regenerate quickly, overgrowth by algae may slow or prevent recovery (Harvell and Fenical 1989, Murdoch 2006).

Nudibranch corallivores

All nudibranchs are carnivores. Historically, little information has been available on the relationships between feeding mechanisms and prey type among nudibranchs. However, several papers have focused on nudibranch diets since the 1960’s (e.g., McDonald and Nybakken 1978, 1997, 1999). Todd (1981) identified four trophic groups,

those feeding on sponges, bryozoans, hydroids, and a miscellaneous category which includes other cnidarians. Hydroids represent the largest trophic category. A wide array of morphological forms and feeding mechanisms exist among the several major subgroups of nudibranchs. If correlations can be found between any of these taxa and specific prey, predictions may be made about prey and feeding mechanisms of unstudied or newly discovered species.

Phylum Mollusca

Mollusca is one of the largest phyla of marine invertebrates, second only to the Arthropoda. Estimates of living marine species vary widely, from 50,000 to 75,000 (Bouchet 2006). Molluscs are characterized by an unsegmented, bilaterally symmetrical body without a significant coelomic cavity. Additionally, many molluscs have developed dorsal or lateral shells of calcium carbonate for protection. The majority of molluscs (apart from Cephalopoda) possesses an open circulatory system with a heart and an aorta, and has ctenidium for gas exchange (Hall, E.B. 2002). The phylum contains eight major subdivisions usually treated as classes: Neomeniomorpha (Solenogastres), Caudofoveata, Monoplacophora, Polyplacophora, Gastropoda, Bivalvia, Scaphopoda and Cephalopoda.

Class Gastropoda

Gastropoda is the largest and most diverse molluscan class with 60,000 to 80,000 living species by some estimates (Bouchet & Rocroi 2005), including limpets, conchs, cowries, whelks, nudibranchs, sea hares, slugs and abalones. The name means “stomach

foot”; the foot being the large ventral structure used for crawling, swimming, burrowing or even enveloping prey. Gastropods include grazers, browsers, planktivores, scavengers, detritivores and active carnivores. Most have a well developed head with rudimentary eyes, tentacles, and concentrated ganglion (Hall, 2002). Additionally most have a coiled shell, which has been independently lost in several groups, including the nudibranchs (although shells are not unique to the Gastropoda among the Mollusca). One of the basic distinguishing features of the Gastropoda is the phenomenon of torsion, the 180° counter-clockwise twisting of the organs during development, which results in the re-positioning of the anal and renal openings and mantle cavity to the anterior of the body. This results in the loss of mantle cavity on one side. The classification of the Gastropoda was revised by Bouchet & Rocroi (2005) and is based on a hybrid of cladistic research and the more traditional Linnaean taxonomical system.

The most up to date system of Bouchet and Rocroi will be used in this paper. Accordingly, nudibranchs are classified under the clade Heterobranchia which contains the informal groups Pulmonata, Lower Heterobranchia and Opisthobranchia. Nudibranchia is a subclade under Nudipleura, and is itself divided into two main clades, Dexiarchia, and Euctenidiacea. Dexiarchia includes clades Pseudoeuctenidiacea (with the sole superfamily Doridoxoidea) and Cladobranchia (with subclades Euarminida, Dendronotida and Aeolidida as infraorders). Euctenidiacea contains Doridoidea and Gnathodoridacea.

Clade Heterobranchia ("different-gilled snails")

Heterobranchia is one of the main clades of Gastropoda and represents all terrestrial, freshwater and marine snails and slugs. It contains the largest number of species in the Gastropoda.

Informal Group Opisthobranchia

Almost all opisthobranchs are marine and have evolved toward shell reduction or complete shell loss. There has been elaboration of the head and various chemical defense mechanisms instead. Additionally, they undergo *detorsion* as opposed to torsion, which characterizes other gastropods, during development. Most opisthobranchs are hermaphroditic. They rely on specialized sensory organs including oral tentacles, and rhinophores which are located close to the head, which has led to a larger brain (Gosliner 1987).

Subclade Nudibranchia

Nudibranchia and Pleurobranchomorpha fall under the clade Nudipleura. All nudibranchs lack shells and possess external gills that may take the form of a plume located near the anus, fingerlike extensions called cerata, or extra skin flaps or ruffles to increase surface area for oxygen absorption. There are several clades and subclades of nudibranchs, and they exhibit a wide range of forms (fig. 3). Although they are hermaphroditic, they do not fertilize themselves. Nudibranchs are famous for their

aposematic coloration (warning colors advertising their toxicity), which makes many species particularly vivid. Potential predators such as fish recall negative encounters with intended nudibranch prey, once engulfing, then spitting them out-- dissuaded by the sequestered nematocysts. Thus, many nudibranchs are bold and conspicuous in behavior as well as coloration. However, not all of them rely on this defense strategy; some species use cryptic coloration or escape swimming behavior to avoid predators. Crypsis defense may be established through the uptake of dyes from their prey, while other nudibranchs have developed morphological structures that mimic their prey/substrate (Gosliner 1987). Nudibranch body forms vary greatly but all exhibit bilateral symmetry. Nudibranchs develop from an egg ribbon usually deposited on the prey item. All opisthobranch veligers have shells initially, but upon reception of chemical stimulus from its prey, nudibranch veligers undergo metamorphosis and lose their shells. Some species will remain on the colony upon which they hatched; but some planktotrophic species, through chemotaxis, have a remarkable ability to home in on and settle upon the food source upon which they will live and feed. However, in the case of corallivores, there is the possibility that the tiny veligers could themselves become prey of the coral polyps (Gosliner 1987).

Clade Euctenidiacea

Also known as Anthobranchia, this clade contains Gnathodoridacea and Doridoidea (distinct from the Doridoida below) and is distinguished by a circular plume of gills near the posterior of the mantle.

Clade Dexiarchia

This clade contains the Pseudoeuctenidiacea and Cladobranchia, which together contain the four main nudibranch groups below (Fig. 3):

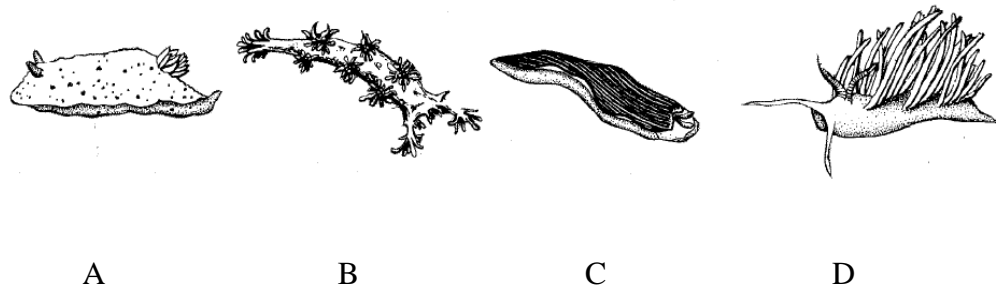


Fig. (3) Typical body plans of nudibranch subclades. A) Doridoida, B) Dendronotida, C) Euarminida, D) Aeolidida (Bertsch 1984c).

a. Subclade Doridoida (Pseudoeuctenidiacea)

This is the largest of the clades under Dexiarchia with more species than all the others combined. It is the only subclade under Pseudoeuctenidiacea. A plume of gills surrounds the anus on the posterior (notum). They eat sponges, bryozoans, polychaete worms, ascidians, and other opisthobranchs. This group includes the superfamilies Doridoidea, Phyllidioidea, Onchidoridoidea, and Polyceroidea.

b. Subclade Dendronotida (Cladobranchia)

This group exhibits rhinophores with a cuplike sheath and a row of gills along the notum. They eat only cnidarians and have well developed jaws. This group includes the

single superfamily Tritonioidea, which includes the families Tritoniidae, Aranucidae, Bornellidae, Dendronotidae, Hancockiidae, Lomanoridae, Phylliroidae, Scyllaeidae, and Tethydidae.

c. Subclade Euarminida (Cladobranchia)

This is the smallest subclade. Members possess flattened body shapes and an expanded oral veil on the head. They eat soft corals, sea pens and bryozoans. This group includes the single superfamily Arminidea, with families Arminidae and Doridomorphidae.

d. Subclade Aeolidida (Cladobranchia)

As the second largest suborder, aeolids exhibit digestive projections called cerata along the dorsal mantle, which house nematocysts and zooxanthellae sequestered from cnidarian prey (Rudman 1981, Slatterly 1998). Long and slender, aeolids obtain oxygen through diffusion. They possess strong chitinous jaws and a radula with only a single radial tooth per row. Aeolids have a varied diet including sea anemones, corals, gorgonians, and jellyfish, but they mostly eat hydroids. This group includes: superfamily Flabellinoidea with families Flabellinidae, and Notaeolidiidae; superfamily Fionoidea with families Fionidae, Calmidae, Eubranchidae, Pseudovermidae and Tergipedidae, and superfamily Aeolidioidea with families Aeolidiidae, Facelinidae, Glaucidae, and Piseinotecidae.

Morphology of Feeding Organs

Nudibranch feeding structures include the jaws, oral veil, odontopore, radula and radular musculature, all contained within the buccal mass, the anterior most part of the digestive tract (Fig. 4). The radula is a ribbon-like organ used for feeding by grating, rasping, and cutting. It is a membrane lined with chitinous teeth arranged in differentiated rows: a median or central rachidian tooth flanked by laterals, which are flanked by marginals (Figs. 5 & 6). The number of teeth, their arrangement and shape differ and may be based on the nudibranch's prey. Each tooth has cusps of different shapes and sizes (McDonald 1984), and may be described as hooked, curved, triangular, etc., and they may be serrated or possess denticles. A complex series of muscles control the radula as it protracts and maneuvers the teeth into position to scrape, pierce, cut or tear (Garcia & Gomez 1990).

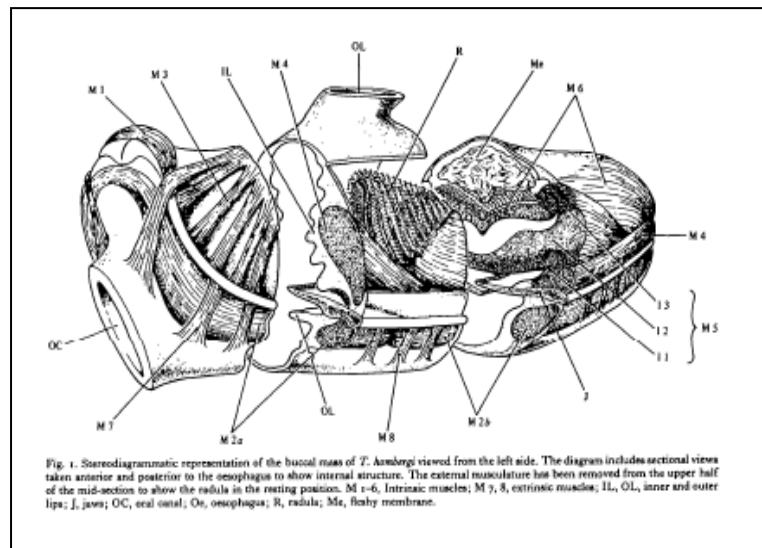


Fig. (4) Detail of the buccal mass structure of *Tritonia hombergi* (Bulloch and Dorsett 1978).

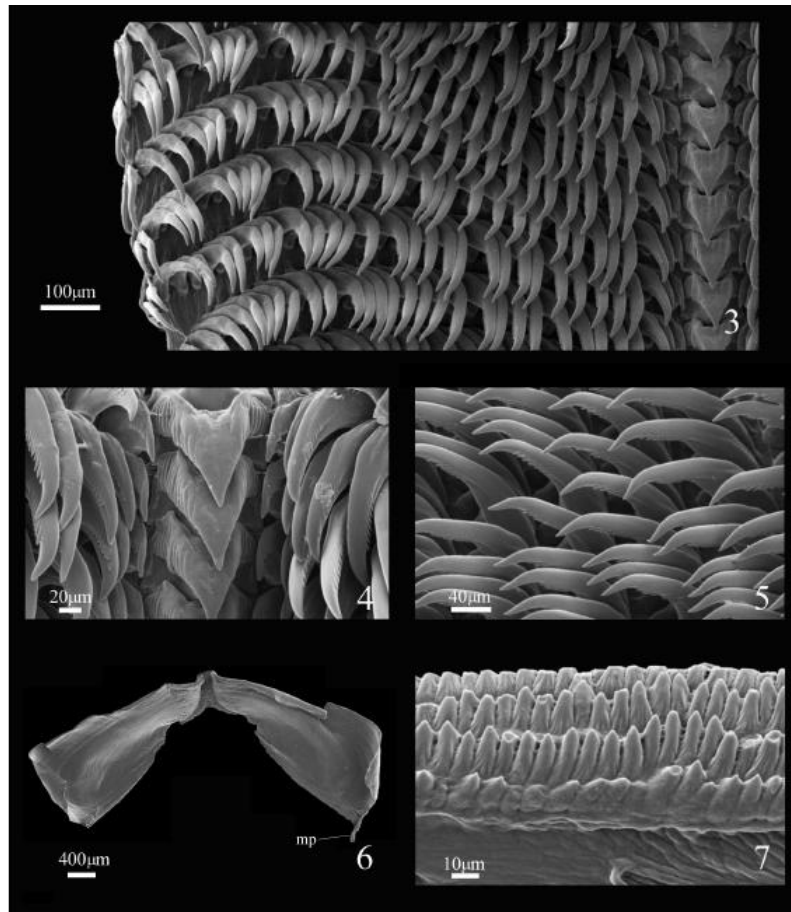


Fig. (5) Radular morphology and jaws of *Armina juliana* (Nestor et al 2002).

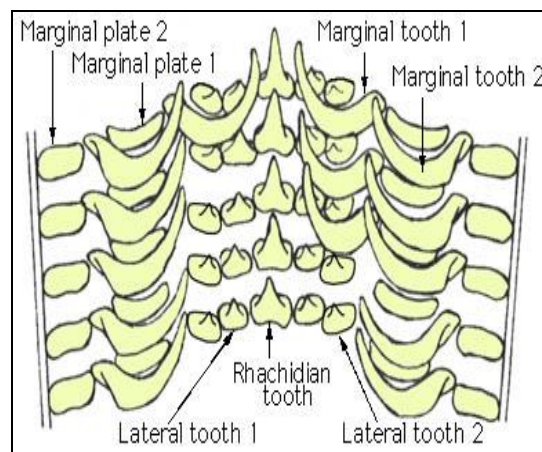
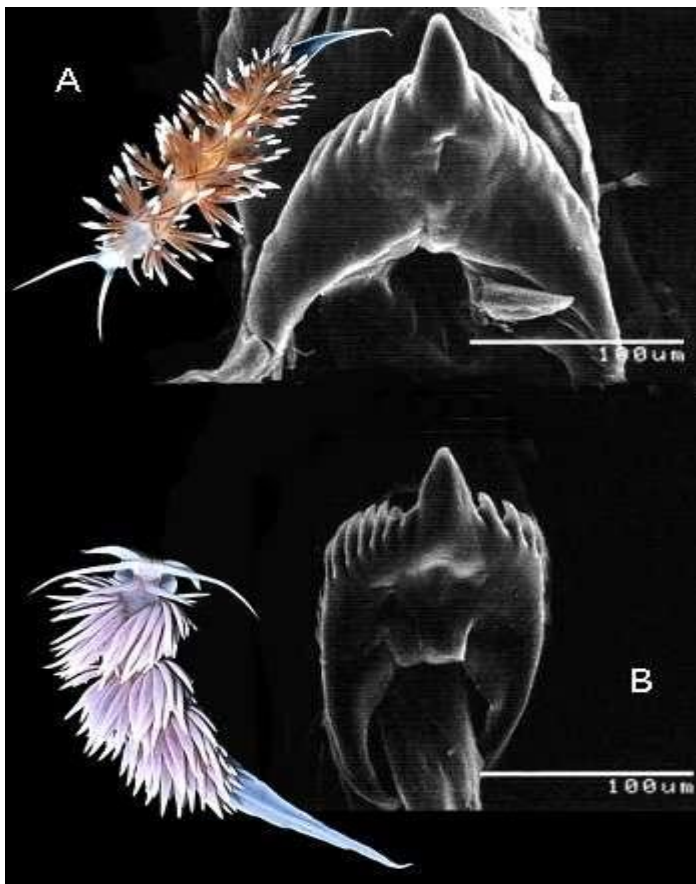


Fig. (6) Illustration of radular tooth arrangement (www.tolweb.org).

Radulas in the literature are described by a formula which describes the number, type, and position of the teeth in each row on the radula. For example, a formula of 3+D+2+R+2+D+3 indicates that the radula has a central rachidian tooth (=R), which is flanked on each side by two lateral teeth, one dominant lateral tooth (=D) and 3 marginal teeth. Additionally, radulas are often referred to as “broad” or “narrow” as in Nybakken and McDonald (1981), and the number of teeth per row ranges from 1 (as in *Aeolidia papillosa*) to 625 (as in *Tochuina tetraquerta*). Nybakken and McDonald (1981) treated a radula with fewer than 20 teeth per row as “narrow” and one with more than 20 teeth per row as “broad”.



The radula can be a valuable taxonomic tool and has been used as such (Bertsch 1977). For example, the nudibranchs *Sakuraeolis gerberina* (Facelinidae) and *S. sakuracea* are easily differentiated by color in their natural habitat; however, preserved specimens lose their color and are indistinguishable. The differences in the teeth are clearly noticeable (Fig. 7).

Fig. (7) Detail of animal and radular tooth of **(A)** *Sakuraeolis gerberina*, and **(B)** *Sakuraeolis sakuracea*

(www.seaslugforum.com) PHOTOS: Yoshi Hirano 1999.

The radula can be used as a taxonomic tool, as above, but varies ontogenetically in several nudibranch species such as *Polycera aurantiomarginata*, found in Spain. Martinez-Pita et al (2006) showed that the radula of this nudibranch species changes with the length of the specimen, in terms of the length of the radula itself, the number of teeth per row and the length of the outer lateral teeth. They describe a “typical” radula with the formula 8-15 x 4+2+0+2+4, four quadrangular marginal teeth without cusps, and no rachidian tooth. Animals between 1.5-2 mm lack a “typical” radula but rather have a “pre-radula”-which distinguishes first teeth rows from the remaining rows. At 3-4 mm they possess both the pre-radula as well as the typical one. Specimens larger than 4mm have a typical, single structure. It was uncertain if the diet of *P. aurantiomarginata* changed also, but the authors speculated that it was possible as the smallest nudibranchs were found on the bryozoan *Sessibugula barrosoi*, while the largest were found on *Bugula neritina*.

Other feeding structures of note include the oral veil (Fig.8), a fleshy hood-like structure that extends beyond the head with sensory papillae on its outer edge; the inner and outer lips that surround the mouth (Fig.9), and a pair of oral tentacles used to detect food odor gradients. The jaws are chitinous plates that may be denticulate in some species. Although *Tritonia*, the most primitive of living nudibranchs, has both jaws and radula, some species such as *Dendrodoris nigra*, have lost the radula and odontophore and feed on sponges using a sucking pharynx (Young, 1966).

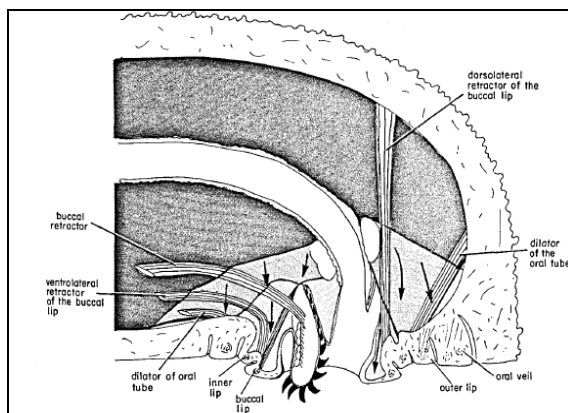


Fig. (8) *Onchidoris billamellata*. Sagittal section of the head during feeding cycle (Crampton 1977).

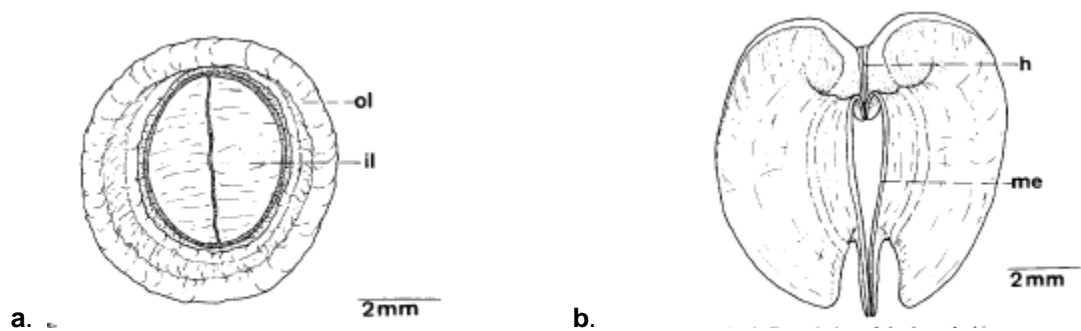


Fig. (9) **a.** Detail of oral cavity, inner lip and outer lip of *Armina maculata*. **b.** Jaws of *A. maculata* (Garcia & Garcia- Gomez 1990).

Prey Selection

To ascertain whether nudibranchs feed on octocorals, investigators employ several techniques. Diet can be determined by stomach content analysis or observations of prey eaten in the laboratory; but direct observation of feeding in the field is best. Still, many records about prey are circumstantial and based on the observation of a species on particular substrate.

Nudibranch prey can be confirmed by three criteria: 1) association of the nudibranch with the prey in the field, 2) occurrence of prey artifacts in the alimentary tract or feces of the nudibranch, and 3) subsistence of the nudibranch on this prey in the lab. The inherent error in using only one criterion is eliminated if all three can be verified. However, even stomach content analyses may not produce clear results. Aboul-Ela (1959) only rarely found spicules of alcyonacean species such as *Heteroxenia fuscescens* (Ehrenberg, 1834) in the gut of *Phyllodesmium xeniae* and suggested that lack of gut contents may be an adaptation to the nudibranchs slow lifestyle—browsing slowly on only a minimal amount of food with the material digested as soon as it is ingested.

Despite the historical difficulty in prey determination, some broad trophic relationships have been determined. For example, all *Phyllodesmium* species (Rudman 1991) and all *Tritonia* species feed on octocorals (Gomez 1973). Table 1 represents a comprehensive list of the known octocoral prey of *Tritonia*.

Species	Prey	References
<i>Tritonia bayeri</i>	<i>Briareum asbestinum</i> ; <i>Leptogorgia virgulata</i> ; <i>Pseudopterogorgia</i> sp.	McDonald and Nybakken 1996
<i>Tritonia bollandi</i>	<i>Verrucella aurantia</i>	Smith and Gosliner 2003
<i>Tritonia challengeriana</i>	<i>Alcyonium antarcticum</i>	Wägele 1995
<i>Tritonia diomedea</i>	<i>Ptilosarcus gurneyi</i> ; <i>Stylatula elongata</i> ; <i>Virgularia</i> sp.	McDonald and Nybakken 1996, 1999; Wyeth et al. 2006; Behrens 2007
<i>Tritonia festiva</i>	<i>Clavularia</i> sp.; <i>Discophyton rudyi</i> ; <i>Gersemia fruticosa</i> ; <i>Gersemia rubiformis</i> ; <i>Leptogorgia chilensis</i> ; <i>Ptilosarcus gurneyi</i>	McDonald and Nybakken 1996, 1999; Goddard 2006
<i>Tritonia griegi</i>	<i>Paramuricea placomus</i>	McDonald and Nybakken 1996, 1999
<i>Tritonia hamnerorum</i>	<i>Gorgonia flabellum</i> ; <i>Gorgonia ventalina</i>	McDonald and Nybakken 1996, 1999
<i>Tritonia hawaiiensis</i>	<i>Anthelia edmondsoni</i>	McDonald and Nybakken 1996, 1999
<i>Tritonia hombergi</i>	<i>Alcyonium digitatum</i> ; <i>Antennularia</i> sp.	Bullock and Dorsett 1979; McDonald and Nybakken 1996, 1999
<i>Tritonia incerta</i>	<i>Alcyonium aurantiacum</i>	McDonald and Nybakken 1996, 1999
<i>Tritonia lineata</i>	<i>Kirchenpaueria pinnata</i> ; <i>Sarcodictyon catenata</i>	McDonald and Nybakken 1996, 1999
<i>Tritonia manicata</i>	<i>Cornularia cornucopiae</i> ; <i>Clavularia</i> sp.	McDonald and Nybakken 1996, 1999
<i>Tritonia myrakeenae</i>	Gorgonians and octocorals (not identified)	Camacho-Garcia et al. 2005
<i>Tritonia nilsodhneri</i>	<i>Eunicella verrucosa</i> ; <i>Eunicella singularis</i> ; <i>Leptogorgia sarmentosa</i>	McDonald and Nybakken 1996, 1999
<i>Tritonia odhneri</i>	<i>Leptogorgia platyclados</i> ; <i>Primnoella divaricata</i> ; <i>Primnoella scotiae</i> ; <i>Renilla octodentata</i> ; <i>Stylatula</i> sp.; <i>Tripalea clavaria</i>	Schrödl 2003; present work
<i>Tritonia papalotla</i>	<i>Epizoanthus</i> sp.	Bertsch et al. 2009
<i>Tritonia plebeia</i>	<i>Alcyonium digitatum</i> ; <i>Alcyonium siderium</i> ; <i>Eunicella verrucosa</i> ; <i>Leptogorgia</i> (<i>Lophogorgia</i>) <i>sarmentosa</i> ; <i>Obelia geniculata</i> ; <i>Paramuricea placomus</i> ; <i>Halecium</i> sp.	Allmon and Sebens 1988; McDonald and Nybakken 1996, 1999
<i>Tritonia pickensi</i>	<i>Leptogorgia chilensis</i> ; <i>Psammogorgia arbuscula</i> ; <i>Muricea</i> sp.	McDonald and Nybakken 1996, 1999; Camacho-Garcia et al. 2005
<i>Tritonia striata</i>	<i>Paralcyonium elegans</i>	McDonald and Nybakken 1996, 1999
<i>Tritonia vorax</i>	<i>Pachyclavularia cylindrica</i>	McDonald and Nybakken 1996, 1999
<i>Tritonia wellsi</i>	<i>Gorgonia ventalina</i> ; <i>Leptogorgia virgulata</i>	McDonald and Nybakken 1996, 1999

Table (1) Summary of known dietary interactions of *Tritonia* species (García-Matucheski & Muniain 2010).

Although most nudibranchs are monophagous, that is, they feed on only one prey species, exceptions exist. Several *Tritonia* species, such as *T. diomedea*, *T. plebeia* and *T. festiva*, prey on multiple octocoral species (Table 1). Nybakken & McDonald (1981) recorded ontogenetic prey switching in *Dendronotus iris*. Juveniles prey upon the thecate hydroid *Obelia commissuralis*, while adults feed on the burrowing anemone *Pachycerianthus fimbriatus*, which may reduce intraspecific competition among sizes. Similarly, *Onchidoris billamellata* eats bryozoans as juveniles and acorn barnacles as adults (Thompson and Brown, 1984). Feeding experiments including direct observations and gut contents determined that *Tritonia festiva* lives and feeds on the pink gorgonian



Lophogorgia chilensis in La, Jolla, California (Fig.10), but subsists exclusively on the sea pen *Ptilosarcus guernei* to the north in Puget Sound, despite no mention of any differences in radular morphology in the different locations (Gomez,1973).

Fig. (10) *Tritonia festiva* on *Lophogorgia chilensis* (www.seaslugforum.com).

Aboul-Ela (1959) performed stomach content analysis on *Phyllodesmium xeniae* and found spicules of alcyonarian species such as *Heteroxenia fuscescens*. Finding such evidence was a rare occurrence, however. It was suggested that lack of food in the gut may be an adaptation to the nudibranchs slow lifestyle- browsing slowly on only a minimal amount of food, the material is digested as soon as it is ingested, providing another difficulty in food determination.

As noted earlier, documented changes in radular morphology due to prey switching or ontogeny provide another complication. Nybakken and Eastman (1977) found that juvenile *Triophia maculata* had one marginal tooth on the radula and fed on encrusting bryozoans, while adults, with 4-8 marginal teeth, fed on encrusting and arborescent bryozoans.

In many past food studies, correlations may have been obscured by investigators not knowing if a particular nudibranch is a juvenile, or neglecting to check if the radula of the juvenile and the adult were the same, as in a report on *Dendronotus iris* by Cooper (1979). Differences were found between the diets of juveniles and adults, but radular

differences were not taken into account. These complications led to some assertions that radular morphology may not be the best indicator of diet. Cattaneo-Vietti & Boreo (1988) determined that diet in aeolids is not strictly correlated with radular morphology. After observing the nudibranch *Facilina bostoniensis*, normally associated with athecate hydroids such as *Tubularia larynx* and *Clavia multicornis*, feeding on the sea pen *Virgularia mirabilis*, Everston and Bakken (1999) suggested that nudibranchs may not be as stenophagous as previously believed. Because radular morphology may change with growth, some (Martinez-Pita *et al* 2006) believe that size may be a better indicator of feeding method and diet.

Comparison of feeding structures

One of the most important factors in the development of nudibranch anatomy is food source. This section will provide examples of the relationship between morphology and prey. Both body shape and radular morphology have co-evolved with prey species (Behrens 1991). In general, the more filamentous and articulatory (soft and flexible, thin) the prey, for example, the narrower the radula (Behrens 1991). Nybakken and McDonald (1981) found correlations between nudibranch radula type and diet, and also noted variations among predators of tunicates, bryozoans, and hydroids. However, Cattaneo-Vietti and Balduzzi (1991) found that the nudibranchs with the thinnest radulas fed on the hardest organisms.

Sponge feeders such as *Platydoris argo* (Megina *et al* 2002), tend to be bulky and flattened, and employ cryptic camouflage, mimicking their prey (Diveoz.com). Sponge

feeders have many rows of teeth used to rasp and scrape the surface like a rake, while anemone predators have a broad central tooth with many denticulations. Aeolids prey mainly on hydroids and have a large chitinous jaw and a radula with teeth reduced to a single central row (Behrens 1991).

The following nudibranchs provide examples of the similarities and differences in feeding structure morphology in relation to diet. The presence of jaws; the number, shape, length, angle of curvature, and orientation across the radula of the teeth; the distance between the rows, as well as the overall shape of the radula itself, may all be determined by the nature of the prey. Nybakken and McDonald (1981) compared the radular morphology of several West American nudibranchs that feed of bryozoan, cnidarian, and ascidiacean prey (Table 2).

Nudibranch species	Teeth per row	Broad or narrow	Anthozoa						Other food
			Actini-aria	Cerian-tharia	Stolo-nifera	Pennatu-lacea	Gorgo-nacea	Alcyo-nacea	
<i>Tritonia diomedea</i>	117–193	broad				X			
<i>Tritonia festiva</i>	36–72	narrow			X	X	X		
<i>Tochuina tetraquetra</i>	328–625	broad				X		X	
<i>Dendronotus frondosus</i>	13–23	narrow							Ascidacea
<i>Dendronotus iris</i>	23–43	narrow		X					
<i>Armina californica</i>	81–163	broad				X			
<i>Dirona picta</i>	5	narrow							Bryozoa
<i>Coryphella iodinea</i>	3	narrow							Ascidacea
<i>Phidiana crassicornis</i>	1	narrow				X			Ascidacea
<i>Aeolidia papillosa</i>	1	narrow	X						
<i>Aeolidiella takanosimensis</i>	1	narrow	X						
<i>Cerberilla mosslandica</i>	1	narrow	X						
<i>Spurilla oliviae</i>	1	narrow	X						
<i>Spurilla chromosoma</i>	1	narrow	X						
<i>Antipella barbarensis</i>	29–45	narrow							Bryozoa

Table (2) Some radula characteristics of nudibranchs consuming anthozoans and other invertebrates.

Dendronotacean nudibranchs, which include the families Tritoniidae, Aranucidae, Bornellidae, Dendronotidae, Hancockiidae, Lomanoridae, Phylliroidae, Scyllaeidae and Tethydidae, all have radulas with similar individual teeth: strong laterals and curved marginals. Members of the Tritoniidae have a well developed central tooth with many laterals, so they possess a broad radula to accommodate them (McDonald 1983).

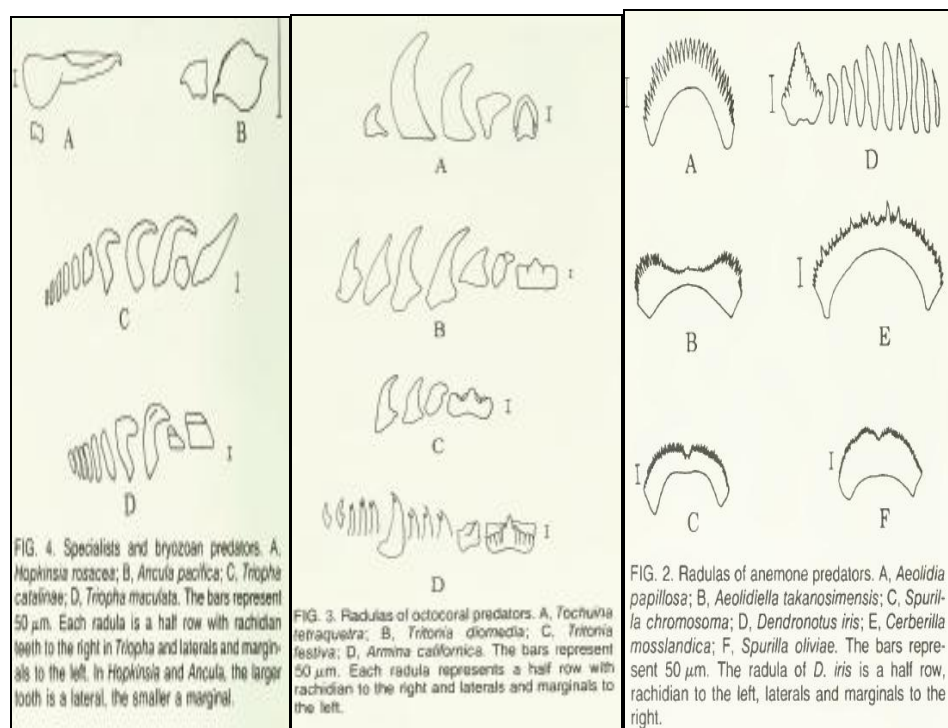
Marioniopsis fulvicola, a specialist predator of the alcyoniid soft coral *Parerythropodium fulvum fulvum* in the Red Sea (Fig. 11), has strong broad jaws with coarse denticles, and a broad tricuspid median tooth. This species has yellow-brown and grey morphs which have cerata that mimic its prey. Usually one, one nudibranch per colony is observed (Avilla 1999).



Fig. (11) *Marioniopsis fulvicola* on *Parerythropodium fulvum fulvum* (www.seaslugforum.com).

Among the species investigated by Nybakken and McDonald (1981), three members of the Tritoniidae, *Tochuina tetragueta*, *Tritonia diomedia*, *Tritonia festiva*, and the arminid *Armina californica*, specialize on octocorals. All have many teeth per row and a broad radula. *Tritonia* species are characterized by the absence of stomach plates, undivided digestive glands, a radula with tricuspid rachidian teeth, blunt differentiated first lateral teeth, and simple hamate (hook-shaped) outer laterals (Smith & Gosliner 2003). Although all are octocoral specialists, slight differences in denticulation and other structures may be related to their different octocoral diets (Fig 12).

Armina californica differs from the others in that its teeth have bifid tips and are less massive. *T. festiva* is another exception in that it is small and eats stoloniferans such as *Clavularia* spp., which are smaller than the prey of the other nudibranchs, even smaller than the nudibranch itself. Nybakken and McDonald (1981) claim that this explains its unusually narrow radula. However, both *T. festiva* and *T. diomedia* eat *Ptilosarcus guerney* (Gomez 1973), a sea pen that is considerably larger than stoloniferans, which is inconsistent with the contention that *T. festiva* possesses markedly different buccal structures due to its diet. Still, radular morphology *may* be plastic with diet. In a study of radular plasticity in the snail *Lacuna*, Padilla (1998) found that, as the radular teeth were constantly regenerating, changes in diet produced differently shaped teeth.



a.

b.

c.

Fig. (12) Radulas of (a) bryozoan predators, (b) octocoral predators and (c) anemone predators (McDonald and Nybakken 1981).

Other *Tritonia* not mentioned by Nybakken and McDonald (1981) include *T. bollandi* of Okinawa, which possesses a radula that has a tricuspid rachidian tooth with a differentiated first lateral tooth and a series of hamate to falcate lateral teeth. Its buccal armature consists of jaws with 2-4 rows of microscopic denticles along the masticatory border (Smith and Gosliner 2003).

Tritonia hamnerorum has well developed oral glands which surround the dorsal, lateral, and ventral surface of the buccal mass. It possesses thin, elongated jaws, a long masticatory border, and six rows of pointed teeth on the radula. Rachidian teeth are tricuspid, with an acute central cusp (Gosliner & Ghiselin 1987).

Tritonia hombergi has strong chitinous jaws that extend the length of the buccal mass; they are hinged anteriorly and have serrated cutting edges. The radula is divided into two sets of cutting lobes with two sets of cutting muscles and is used for grasping and manipulation rather than rasping. The inner lips are fleshy pads, and the outer lip encircles the buccal mass aperture (Bulloch & Dorsett 1979).

By contrast with the tritoniids, aeolids such as Aeolidiidae, Embletoniidae, Eubbranchidae, Fionidae, Flabellinidae, Glaucidae and Tergipedidae have few rows of 1 or 2 hooked teeth per row. However, they have well developed jaws. Their feeding strategy is to crop and hold cnidarians as they rasp (Behrens 1991). In dorids, the lateral teeth are well developed while the central tooth is not.

In another case for radular correlation with feeding methodology, Lambert (1991) documented the coexistence of 4 different species of nudibranch on the hydroid *Obelia geniculata*: *Dendronotus frondosus*, which has a multi-seriate radula and bites polyps on the hydrocauli towards the center; *Doto coronata*, a suctorial feeder with a flat, uniseriate radula that penetrates the stolons on the edge of the colony; *Eubbranchus exiguous*, which penetrates the hydrothecae with a triseriate radula, and *Tergipes tergipei*, which has a curved uniseriate radula and rakes naked tissue around the hypostome. Although these species feed on the same prey, they have different radular morphologies and feeding behaviors, and occupy and feed on different areas of the colony.

Feeding Strategies

Nudibranchs have different approaches to capturing and ingesting prey. Strategies include suctorial feeders such as *Doto coronata* (Lambert 1991), rasping

feeders such as *Chromodoris hamiltoni* (Gosliner 1987), and bite strikers such as *Tritonia diomedia*, which uses lunging behavior to outmaneuver its sea pen prey (*Ptilosarcus gurneyi*), which can quickly withdraw into the sediment when disturbed (Wyeth 2006).

Figure (13) shows typical a gastropod feeding cycle, the repeated process of ingestion. The diagram for the snail *Lymnaea* is used as a generalized example of the cyclical movement involving radular protraction, rasping, retraction and swallowing. This is highly variable, however; some nudibranchs, such as *Tritonia hombergi*, use strong jaws to bite first and use the radula to usher food into the esophagus. *Doto coronata* uses its radula to pierce hydroids, creating a hole through which it can suck fluids.

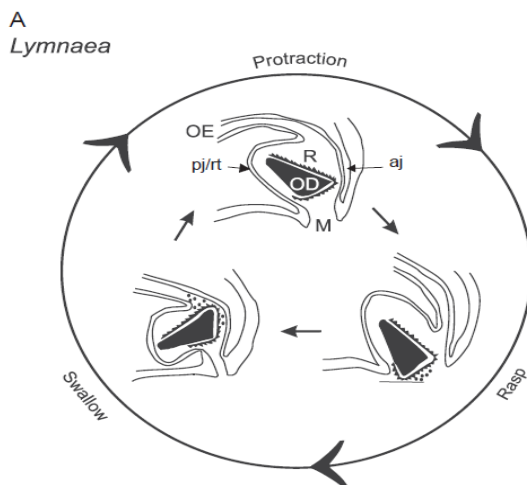


Fig. 2. Feeding movements of (A) *Lymnaea* and (B) *Aplysia*. (A) Schematic diagram of the feeding sequence of *Lymnaea* in which the three phases of movement (protraction, rasp and swallow) are shown diagrammatically. The muscles of the buccal mass – principally the anterior and posterior jugalis (aj, pj) and radular tensor (rt) – contract, squeezing and rotating the odontophore (OD). This is covered by the many-toothed radula (R), which is rasped across the substratum. Food particles are then collected and passed into the oesophagus (OE). M, mouth. After Benjamin and Elliott (1989). (B) A biting sequence in

Fig. (13) Diagram of *Lymnaea* feeding cycle (Elliott and Susswein 2002).

Miller (1962) suggested two general nudibranch life cycles that reflect feeding strategies: 1) short-lived, seasonal animals that eat fast-growing, seasonal prey such as hydroids, or 2) longer-lived nudibranchs with an annual life cycle that eat long lived-prey such as coral and sponges.

Feeding behavior ranges from effective grazing, in which small portions of a colony are ingested, leaving most of the colony alive, to complete predation. Gomez (1973) observed *Tritonia festiva* eating the gorgoniid octocoral *Lophogorgia chilensis* in the lab. The nudibranch lifts its oral veil and spreads it over the branch tip, trimming off 2 mm with the bite. Then, it strips the coenenchyme off the remaining stump. This technique may be harmful to the colony as it prepares the way for settlement of fouling organisms such as barnacles and algae. In contrast, Allmon and Sebens (1988) reported that *Tritonia plebia* attacks the base of Alcyonium species in the Atlantic, which causes whole colony mortality.

Figure 14 documents a dramatic predatory event between *Tritonia diomedea* and *Ptilosarcus gurneyi*. This is a swift attack on a prey organism that is capable of evasive movement via rapid retraction into the substrate, unlike other octocorals. Thus, the bite strike and swallowing are separate events carried out by different parts of the buccal mass musculature, because the food must be manipulated before swallowing. Willows (1978) observed that feeding was more important than resting, courtship and copulation in this species, as starved laboratory specimens resumed an active state or disengaged from copulation when presented with food; however, escape-swimming behavior superseded feeding in these trials.

Tritonia diomedea breaks the stalk of its prey into pieces with its radula. (Shaw 1991). By contrast, *Tritonia hombergi* uses its jaws to cut food into sizable pieces to be manipulated by the radula, which is used for grasping and manipulation, rather than rasping. The inner lip is composed of fleshy pads, and the outer lip encircles the buccal

mass aperture. It eats *Alcyonium digitatum* exclusively, and the food is detached by the jaws and moved into the buccal mass by the radula (Bulloch et al 1979a).

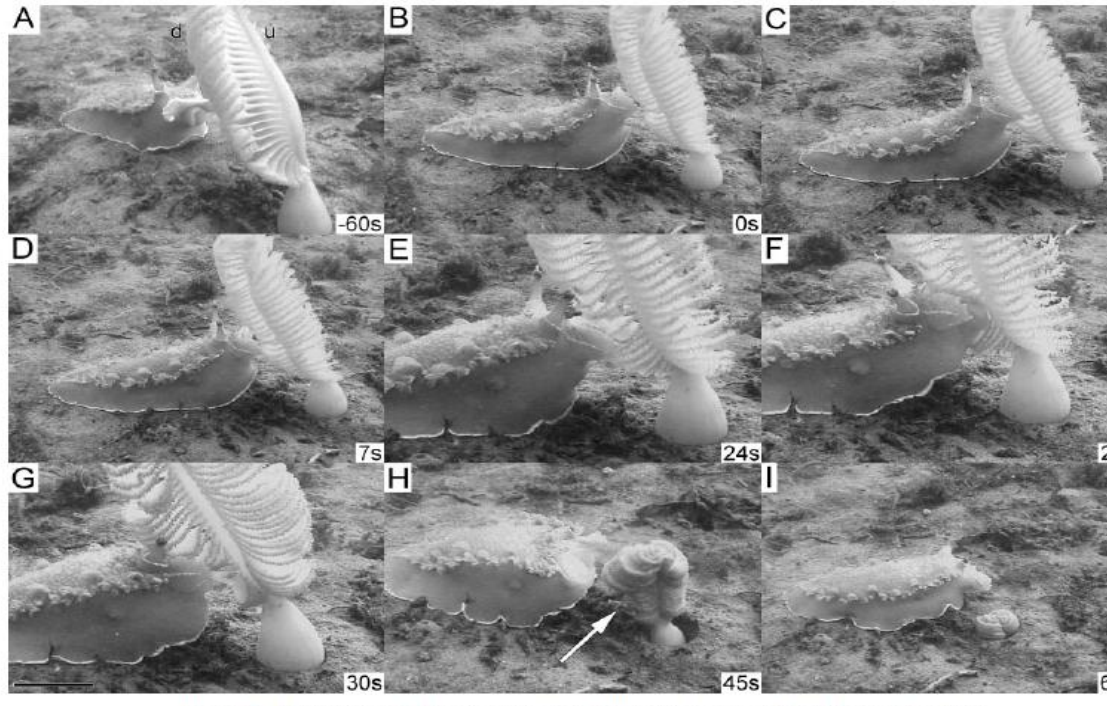


Fig. (14) *Tritonia diomedea* attacking *Ptilosarcus gurneyi* (Wyeth 2006) (A) *T. diomedea* stalks the sea pen from downstream with oral veil lifted. (B) The slug nears prey, stops crawling and lifts its head off of the substratum. (C-D) The tips of the oral veil briefly make contact with the sea pen and is immediately retracted.. (E) The nudibranch prepares to strike by protruding its lips. (F) The jaws are opened, the buccal mass is lunged forward and the radula is extended. (G) The radula is used to grasp a pinnea and pull it into the mouth- at this point the sea pen begins to retract into the sediment. (H) The jaws cut the pinnea, leaving a stump. (I) Having finished the strike, crawling resumes.

Garcia (1990) looked for homologies between the buccal mass of *Armina maculata* and other nudibranchs, mainly *Janolus cristatus*, focusing mainly on musculature. *Armina maculata* was selected because the anatomy of the buccal mass of euarminoidean nudibranchs was unknown, while the anatomy of *Janolus cristatus* had been studied extensively. Several processes link the feeding mechanics of these animals,

including buccal mass protraction and retraction, oral tube dilation, odontophore protraction, the spreading of the radula and the closing of the jaw. These movements in both animals require similar musculature.



Fig. (15) *Armina maculata* (www.seaslugforum.com).

The feeding cycle of *Armina maculata* (Fig.15) was difficult to determine, however. Garcia (1990) suggested that the feeding cycle of unknown nudibranchs could be determined by comparing homologous feeding structures. In this case, *Armina maculata* has a buccal structure similar to *Tritonia hombergi*, which suggests similar ingestive functions.

Both *T. hombergi* and *A. maculata* feed on pennatulaceans. Based on the known feeding cycle of *T. hombergi*, Garcia (1990) suggested three stages in the feeding cycle of *A. maculata*: a) protraction of the buccal apparatus, b) grasping of the prey and rasping of the tissues, c) ingestion of the food.

Locating Prey

Nudibranchs employ a variety of tactics to locate food, such as mechanosensation of water flow, chemoreception, magnetoreception, and photoreception, which in some species is simply visual orientation to dark surfaces (Wyeth 2006), because the eyes of nudibranchs are rudimentary and located deep within the mantle (Conklin 1977). Water flow and odor gradients are crucial to *Tritonia diomedea* in locating its prey, the sea pen *Ptilosarcus gurneyi* (Watson and Chester 1993). *Tritonia diomedea* uses its oral veil tips to detect the direction of the food odor gradient by head waving. Bergh (1894) found that *T. diomedea* bites regularly in response to sea pen extract in the lab. Gentle touching aligns the mouth, as in *Armina californica* (Willows, 1977), and the bite strikes are separate from ingestion with the odontophore. *Dendronotus iris* uses head-waving behavior similar to that of *Tritonia diomedea* in detecting food odor gradients that allow the nudibranch to locate its prey (Shaw 1991).

Summary

Although several authors have compiled information on the food habits of nudibranchs, i.e., (McDonald and Nybakken 1981), no definitive, comprehensive resource identifies definite correlations between nudibranch morphology and prey. Several authors have made connections among smaller taxonomic groups, localities or specific prey. Nybakken and McDonald (1981) concluded that: aeolids feeding on anemones tend to have uniseriate radulas with broad, heavily serrated teeth. Nudibranchs that feed either on ctenostome bryozoans or ascidians have similar radulas, with each half row dominated by a massive lateral tooth. Aeolids that feed on hydroids have uniseriate

or triseriate radulas. Those with uniseriate radulas puncture the perisarc and suck out the coenosarc. Those with triseriate radulas feed directly upon the polyps. Most bryozoan feeders prey upon species that lack calcified fronts. Nudibranchs that feed on Pennatulacea and Alcyonacea have very broad radulas. Those that feed on stoloniferans have narrow radulas. Some specialists, such as *Hopkinsia rosacea* and *Ancula pacifica*, have unique radulas that may be related to the specific prey item.

Several complications cited by the investigators provide a basis for errors. Data records for nudibranch prey may be unreliable because of misidentification of the nudibranchs themselves, and/or the difficulty in properly determining their prey. In some species, the morphology, in addition to the food source, may change due to range, age, and prey availability. Pratt and Grason (2006) reported that *Onchidoris muricata*, a nudibranch found on both sides of the Atlantic, often feeds on the invasive bryozoan *Membranipora membranacea* in the Gulf of Maine, even though it feeds on *Electra pilosa* in Europe. Additionally, current nudibranch taxonomy is inconsistent. In order to raise confidence in feeding studies, more data must be added to support the current base of information.

PART II.

Distribution and density of the corallivorous nudibranch

***Tritonia hamnerorum* on the sea fan *Gorgonia ventalina* in the Florida Keys, USA**

Personal Observation and Field Work

Introduction

As a supplement to this capstone review, several surveys were performed to investigate the behavior, density and distribution of the dendronotid nudibranch *Tritonia hamnerorum* (Gosliner & Ghiselin 1987), a specialist corallivore on the gorgoniid octocoral *Gorgonia ventalina* (Linnaeus 1758), in the Florida Keys (Fig.18). *Gorgonia ventalina* is a flabellate octocoral common on reefs throughout the Tropical Western Atlantic region. Its common name, “purple sea fan”, comes from its distinct purple color, although there are yellow and brown morphotypes (Sterrer 1986). *Gorgonia ventalina* is a suspension feeder that grows as a flexible, upright flat fan up to 1 m across. Fans grow perpendicular to the current to maximize surface area for feeding (Wainwright & Dillon, 1969). To take advantage of the constant water flow, they are most commonly found along the reef margins in turbulent waters (Birkeland 1974b). The nudibranch was observed feeding primarily on *G. ventalina* in surveys of several habitats in Florida and the Bahamas, suggesting that it specializes on this species (Pawlik *et al.* 1987, Van Alstyne & Paul 1992, Cronin *et al.* 1995), although Gosliner & Ghiselin (1987) reported

finding it on *Gorgonia flabellum* as well. *T. hamnerorum* can sequester secondary metabolites from the sea fan for its own defense (Faulkner & Ghiselin 1983).

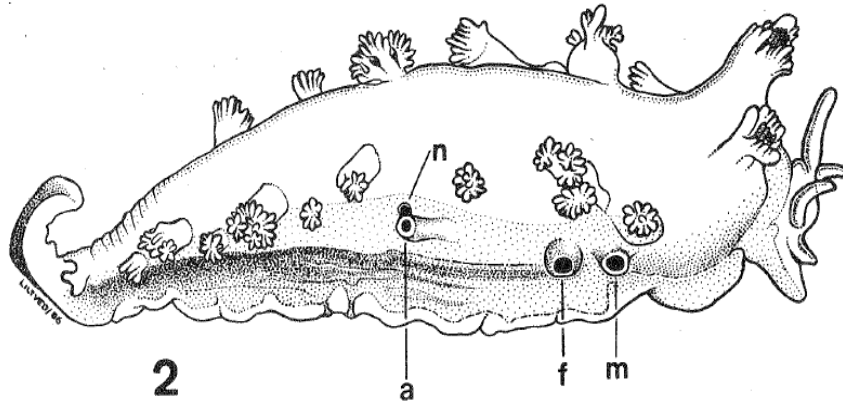


Fig. (16) *Tritonia hamnerorum* Right lateral view of preserved animal; a=anus, f= female aperture, m= male aperture, n= nephroproct, r= rhinophores, o= oral tentacles (Gosliner and Ghislen 1987).

A study of this trophic relationship would improve understanding of molluscan corallivores and serve as groundwork for further studies on the effects of corallivory in the Florida Keys. Investigating the habits of *T. hamnerorum* would help inform the current hypotheses of how and why *T. hamnerorum* outbreaks occur in their normally patchy distribution patterns (Cronin *et al.* 1995). This information may help predict destructive nudibranch outbreaks and provide useful information to environmental managers in the Florida Keys National Marine Sanctuary and John Pennekamp State Park. The increased presence of molluscan corallivores may serve as a bioindicator of reef health, as several opportunistic corallivorous species may take advantage of corals weakened by other environmental stressors (Nagelkerken *et al.* 1997). In particular,

aggregations of large numbers of corallivorous predators may seriously threaten reef communities. Evidence exists that such outbreaks may be related to environmental changes and that they may have become more frequent worldwide over the last decade (Root T. *et al.* 2003). As a result, understanding such outbreaks should broaden knowledge about processes of change on coral reefs, and contribute to resource managers' ability to address them.

During the summer of 2009, fieldwork was conducted at The Florida Keys National Marine Sanctuary in Key Largo to determine the natural distribution of *T. hamnerorum*. Transect surveys were conducted at depths of 1-7 m at sites along several reefs including Grecian Rocks, North Key Largo Dry Rocks, Pickles Reef, French Reef, and Molasses Reef. Sites were chosen based on personal correspondence with park officials and personal observation during pre-planning snorkeling excursions. During preliminary searches in April of 2009, *T. hamnerorum* was discovered on small patches of *Gorgonia ventalina* at densities of 1-10 nudibranchs per fan. These sites contain high concentrations of *G. ventalina*; 50 colonies were estimated in the area ($\sim 20\text{m}^2$) where *Tritonia* was first observed. Adjacent areas surveyed of approximately this the same size had hundreds of colonies. Additionally, these locations were among those surveyed by Cronin *et al* (1995). As a follow up, these sites in Key Largo, FL, were revisited in the summer of 2009 so that any changes in the *T. hamnerorum* population in the area could be assessed, following the methods of Cronin *et al.* (1995).

Background

It is not certain how and why many molluscan corallivores sometimes form aggregations. In the case of *Tritonia hamnerorum*, it is unknown if pelagic veligers settle gregariously on *Gorgonia ventalina* by homing in on chemical cues (Pawlik 1992), or develop and remain on the colony after hatching from egg masses deposited there (Gosliner & Ghiselin 1987). The snail *Cyphoma gibbosum*, which also feeds on *G. ventalina*, may clump together after following mucus trails left by other individuals, leading towards target colonies that are somehow more preferable (Gerhard 1990).

During a brief outbreak in 1992 in the Florida Keys, Cronin *et al.* (1995) carried out the only major study on the trophic relationship between *G. ventalina* and *T. hamnerorum*. The event was considered an outbreak because up to hundreds of



nudibranchs per fan were recorded, whereas maximum recorded numbers previously reached no more than three animals on a single *G. ventalina*. During the 1992 survey, *T. hamnerorum* was found in much greater densities- (means of up to 959 individuals m⁻² of 1-sided sea fan area) (Cronin et al. 1995).

Fig. (17) *Tritonia hamnerorum* on *Gorgonia ventalina* in Bermuda (From Murdoch 2006).

Two months after the initial June surveys, nudibranch densities were much lower and decreased further the following year (Cronin's casual observation- numbers not given). Other sightings have been reported sporadically on internet forums as personal accounts from divers throughout the Caribbean (Rudman 2002).

In another study, Murdoch (2006) in 2005 recorded an unprecedented infestation of *T. hamnerorum* on Devil's Flat, Bermuda, where this species had not been observed before (Fig. 19). The distribution of affected colonies was patchy, and, the outbreak killed approximately half of the gorgonians examined. In addition, Murdoch (2006) noted that *T. hamnerorum* has been found in Honduras, Cayman, Bahamas, and the Florida Keys, in some cases up to 1700 per colony. The highest densities of the nudibranchs were found in the shallow outer reef area, which also maintains the highest population of sea fans. Additionally, on days when the wind was over 15 knots and the seas were rough, no nudibranchs were seen, even at the sites that showed heavy infestation on calm days.

Cronin *et al.* (1995), Murdoch (2006) and the author have all noted seasonal variations in population sizes of *T. hamnerorum*, with sizable (>100 nudibranchs per fan) populations occurring only rarely after November. Murdoch (2006) speculated that colder temperatures and rougher seas might be responsible for their disappearance, as their hold on their gorgonian hosts is tenuous, and they easily lose purchase and fall off in heavy wave action.

Materials and Methods

Study sites included Grecian Rocks, Key Largo Dry Rocks, French Reef, Molasses Reef, Horseshoe Reef, and the Benwood Wreck (Fig 18). A total of eight 50-meter-long transect lines, marked at 5-m intervals, were deployed across the reef at depths of ~3-6m between May and September 2009 in areas heavily populated by sea fans. Field work was suspended due to the disappearance of nudibranchs from 17 October onward. Three transects were run while snorkeling and five on SCUBA. Fans within 1 m on either side of a transect were examined and the numbers of *Tritonia* on each fan counted. Density was determined by counting the nudibranchs on both sides of the sea fan and measuring the maximum width and height of the sea fan. Densities are expressed as numbers of nudibranchs per 1-sided area of the sea fan, with area estimated using the equation for the area of an ellipse [$A = 1/4(\text{width} \times \text{height})\pi$], following the methods of Cronin *et al.* (1995).

Where it was not possible to lay down a transect line (due to time constraints, water conditions or sight irregularities), I made a visual estimation by inspecting as many patches of *Gorgonia ventalina* as possible and noting the presence or absence of *Tritonia hamnerorum* while estimating their numbers.

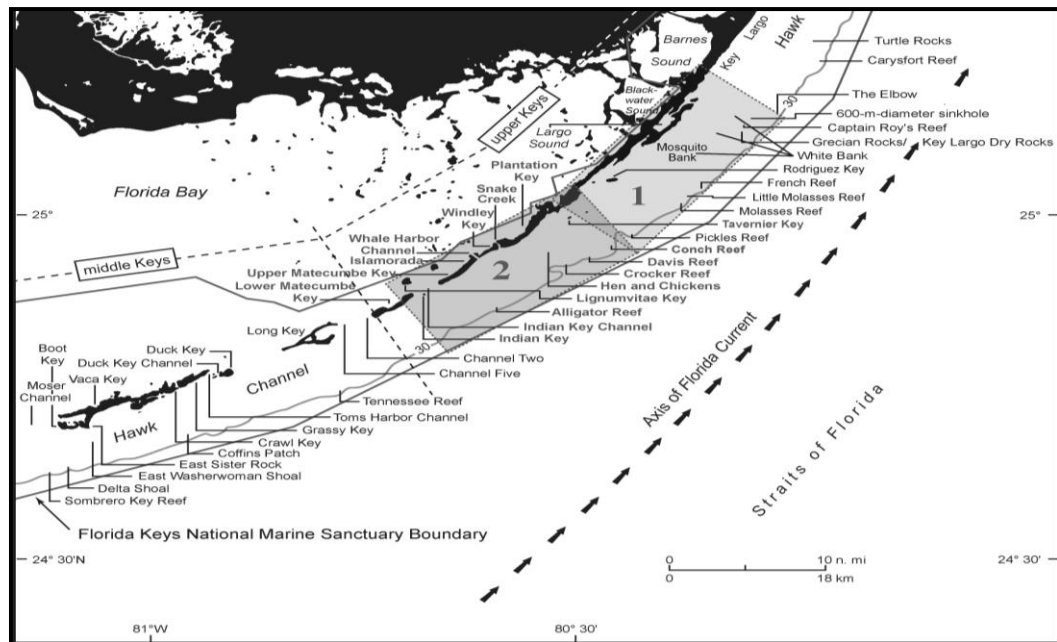


Fig. (18) Area of personal observation in Key Largo, FL (credit: NOAA).

Data and Results

Table 3 lists transect results, including gorgonian density (m^{-2}), percent of gorgonians infested, number of *T. hamnerorum* per sea fan side, and water temperature. Low numbers were found at six of the sites surveyed: ~1-10 *T. hamnerorum* per colony on small, isolated patches (Fig. 19).



During an informal observation at Grecian Rocks, however, >100 individuals per colony were noted at one small 10- m^2 patch containing ~50 fans, comparable to the outbreak levels reported by Cronin *et al.* (1995). The nudibranchs were absent at five other sites.

Fig. (19) *Tritonia hamnerorum* on *Gorgonia ventalina* (Photo by Eric Brown 2007).

Table 3. Record of nudibranchs observed in Key Largo in 2009.

Date	Site	Water temp. °C	Gorgonian density / m ²	% Gorgonian colonies affected	<i>T. hamnerorum</i> per 1 side sea fan (avg.)
6/10/09	Molasses	28.70	20	5	2
6/10/09	Key Largo Dry Rocks	28.70	5	0	0
7/10/09	Benwood Wreck	30.0	?	1	5
7/10/09	French	30.10	15	5	3
7/15/09	French	29.30	15	10	3
7/15/09	French	29.30	15	0	0
7/29/09	French	29.9	3	3	2
7/29/09	Molasses	29.9	20	1	1
10/17/09	Key Largo Dry Rocks	29.0	10	0	0
10/24/09	Key Largo Dry Rocks	28.6	20	0	0
10/24/09	Horseshoe	28.6	15	0	0

The results indicate a greater presence of the animals in the summer followed by a sharp decline as the season advanced into fall. This continued until eventually no nudibranchs were observed.

Conclusion

Tritonia hamnerorum was present on *ventalina* patches in Key Largo, though not in the high numbers witnessed by others (Table 2). In May 2009 during a preliminary scouting run of Grecian Rocks, high densities of nudibranchs were found on patches of sea fans, up to an estimated 50 nudibranchs per colony. Their distribution was patchy: random patches of fans would be occupied by *T. hamnerorum*, while adjacent areas showed no colonization. When the polyps of the sea fans are extended, the colony appears brown; on areas occupied by *T. hamnerorum*, patches of purple ~1 cm across surrounded the nudibranchs, marking the grazed areas. However, it is unknown whether this was due to retraction of the polyps due to disturbance, or if the nudibranchs had actually preyed on those polyps. Additionally, in several colonies, filamentous algae were observed growing on damaged *G. ventalina* colonies, but it was not clear whether the nudibranchs or, perhaps, disease, had caused the damage.

It is clear that *Tritonia hamnerorum* is still present in Key Largo and has the ability to cause significant damage to the local sea fans. The nudibranch seems to appear seasonally and is most abundant in the summer months. These results are consistent with the results of others investigating the distribution and density of *Tritonia hamnerorum* in the Caribbean (Murdoch 2006; Cronin *et al.* 1995).

Discussion

Research began in May and ended in September due to the disappearance of nudibranchs in the area. I found an abundance of *Tritonia hamnerorum* at Grecian Rocks on one dive and fewer on subsequent dives. Although the current study spanned less than

a year, the disappearance of *T. hamnerorum* between July and October is suggestive of seasonality. Cronin et al. (1995) also found a drastic decline in numbers of *T.*

hamnerorum in Key Largo, FL, in fall and winter. Murdoch (2006) noted that the decline in populations of *T. hamnerorum* in Bermuda might be due to colder temperatures and heavy wave action brought on by winter. Because the sea fans remain abundant as a food source all year, it is unlikely that the decline in *T. hamnerorum* numbers can be explained by a reduction in food supply. Another possibility is that they perish immediately after spawning. It remains unclear whether cooler temperatures perhaps combined with rougher waters, or a seasonal life cycle is responsible for their disappearance.

Although the numbers of nudibranchs observed did not rise to the level of population explosion reported by other workers (Murdoch 2006, Cronin et al 1995), numbers in excess of one hundred recorded in May 2009 were followed by a precipitous decline. Aboul-Ela (1959) suggested that nudibranchs migrate or starve due to a reduction in their food supply. As noted above, sea fans remain abundant all year, so the lack of a food source seems an unlikely causative factor. Sea fans are extremely long-lived (60-80 years) while *T. hamnerorum* has a comparatively shorter life-span (unknown) therefore the hypothesis proposed by Miller (1962) that short-lived nudibranchs usually feed on short-lived prey does not apply in this case. Another possibility is that there may be a seasonal variation in the nutritional quality of the gorgonians, and at times it may not be sufficient to support an outbreak.

Summary

Many investigators have focused on the food of nudibranchs since the 1960's, yet very few have attempted to establish relationships between the morphology of their feeding structures, such as the radula and the teeth, and their cnidarian prey. Specific prey preferences may occur within closely related groups of nudibranchs, or feeding strategies and physiology of the nudibranchs may be based on their choice of prey. The type of food has determined the evolution of these structures in the nudibranchs; however, the great variety of feeding types and behaviors makes a comparative study of anatomy difficult.

Understanding the morphology of nudibranch feeding structures does have ecological value, which could lead to conservation policy for marine park managers. Correlations between prey type and nudibranch physiology would aid in predicting the prey of newly discovered nudibranch species through examination of their buccal structures. Some investigators have theorized that several invasive organisms within the range of nudibranch diets, from octocorals to barnacles, may be controlled by introducing nudibranch predators into an environment (Wagner 2007).

Gastropod feeding also has historically provided a model for neurophysiological control mechanisms of nerve impulse patterning, and motor coordination and plasticity (Willows 1978). Studies of nudibranch prey preference, feeding strategies and physiology could provide new insights in this field. Worldwide, from a taxonomic point of view, various suborders share anatomical similarities, but this is not as important as the shared food among different groups. For example, an aeolid and a dendronotid can share similar feeding structures if they share the same food.

Coral reef ecosystems face many threats, including corallivory, which vary in importance. Some corallivores, such as the crown-of-thorns starfish, cause widespread devastation to ecosystems because they completely destroy the colony upon which they feed (Black & Johnson 1984).



Fig. (20) An outbreak of *Tritonia hammerorum* on *Gorgonia ventalina*. Nudibranchs appear as white dots (Murdoch 2006).

Nudibranch corallivores, while mainly monophagous, may cause considerable harm to corals depending on the nature of their feeding (Fig 20). In many cases, the colony is only grazed upon and is able to repair the damage over time. Even so, the damage caused by grazing may provide an opportunity for opportunistic species, such as filamentous algae and barnacles, to settle on the areas that the nudibranch has cleared,

eventually leading to whole-colony mortality. In the event of a corallivore outbreak, however, the results can be devastating to the coral hosts.

On the other hand, nudibranchs may be helpful in controlling threats from organisms that the nudibranchs prey upon themselves. It may be possible to use nudibranchs such as *Phyllodesmium poindimiei* of the Indo-Pacific as biocontrol of invasive species such as *Carijoa riisei*, an octocoral that has invaded Hawaii (Wagner, 2009).

Are octocorals at risk from nudibranch outbreaks? Nudibranchs are partial predators that usually spare the entire colony. A review of the literature has found only two instances of widespread destructive nudibranch corallivory: the case of *Tritonia hamnerorum* feeding on *Gorgonia ventalina* and *G. flabellum* (Cronin *et al.* 1995), and the 1992 outbreak in Bermuda (Murdoch 2006). However, these occurrences were only recently documented. Further study is needed to explain the sudden conspicuousness of *T. hamnerorum* in the western Atlantic since its discovery in 1985.

As environmental conditions change around the world, the range of some species may widen or shrink. Non-native species may migrate or accidentally be introduced into areas where novel food options may cause them to alter their diet and feeding mechanisms. Waters (1973) documented that the nudibranch *Aeolidia papillosa* feeds on different species of anemone in different localities. In another example, *Tritoniopsis elegans* is a generalist octocoral predator; in the lab it fed on *Sinularia densa* and *Sarcothelia edmondsoni* when its preferred prey *Carijoa riisei* was absent (Rudman 1991).

A comprehensive collection of molluscan feeding information could have value in understanding ecological systems, because molluscan corallivores may serve as a bioindicator of reef health (Hallock *et al.* 2004). Table 3 lists a number of nudibranchs and their octocoral prey. Unusually large numbers of these predators can correlate with environmental anomalies such as warmer water temperatures and high nutrient levels, which may be due to anthropogenic disturbances (Harley *et al.* 2006). The study of the relationship between nudibranch corallivores and their octocoral prey has the potential to yield benefits in many fields, and warrants further study.

Table 4. Selected nudibranchs and octocoral prey.

Nudibranch	Location	Prey	Reference
<i>Tritonia plebia</i>	North Atlantic	<i>Alcyonium digitatum</i> <i>Alcyonium siderium</i>	Allmon & Sebens 1988
<i>Tritonia hamnerorum</i>	Caribbean, Western Atlantic	<i>Gorgonia ventalina</i> , <i>Gorgonia flabellum</i>	Cronin et. al 1995
<i>Tritonia festiva</i>	Puget Sound, USA La Jolla, CA, USA	<i>Ptilosarcus gurneyi</i> <i>Lophogorgia chilensis</i>	Birkeland 1974b Gomez 1973
<i>Tritonia belli</i>	Antarctica	<i>Clavularia frankliniana</i>	McClintock et. al 1994
<i>Tritonia plebia</i>	New England, USA	<i>Plexaurella</i> spp.	Allmon & Sebens 1988
<i>Armina californica</i>	Puget Sound	<i>Ptilosarcus gurneyi</i>	Birkeland 1974b
<i>Hermisenda crassicornis</i>	Puget Sound	<i>Ptilosarcus gurneyi</i>	Birkeland 1974b
<i>Tritonia wellsi</i>	Singapore	<i>Leptogorgia virgulata</i>	Goh 1999
<i>Histiomena convolvula</i>	Gulf of California	<i>Muricea</i> spp.	Bertsch 2003
<i>Tritonia nilsodhneri</i>	Atlantic, Africa –Eur.	<i>Eunicella</i> sp.	Gosliner 1987
<i>Armina tigrina</i>	Southeastern USA	<i>Renilla reniformis</i>	Barbsy 2004
<i>Marioniopsis cyanobranchiata</i>	Red Sea	<i>Xenia</i> sp.	Gosliner 1987
<i>Phyllodesmium longicirrum</i>	Indonesia- Australia	<i>Sarcophyton trocheliophorum</i>	Coll et al. 1985
<i>Phyllodesmium guamensis</i>	Guam	<i>Sinularia maxima</i> <i>S. polydactyla</i>	Rudman 1981 Slatterly 1998
<i>Phyllodesmium jakobsenae</i>	Indonesia- Philippines	<i>Xenia</i> sp.	Wägele 2005
<i>Phyllodesmium briareum</i>	West Pacific	<i>Briareum stechei</i> <i>Solenopodium stelleri</i>	Wägele 2005 Sea Slug Forum
<i>Dermatobranchus</i> sp. undescribed	South Africa	<i>Sarcophyton trochiform</i>	Gosliner 1987
<i>Armina maculata</i>	Mediterranean	<i>Verticillium cynomorium</i>	Garcia 1984
<i>Dermatobranchus ornatus</i>	Indo-West Pacific	<i>Muricea</i> sp.	Gosliner 1987
<i>Tritonia diomedea</i>	NE Pacific	Pennatulaceans: <i>Ptilosarcus gurneyi</i> , <i>Stylatula elongata</i> , <i>Virgularia</i> sp.	Wyeth 2006
<i>Dermatobranchus striatus</i>	Red Sea	<i>Clavularia hamra</i>	Aboul-Ela 1959
<i>Tritonia bollandi</i>	Okinawa	<i>Ellisellidae</i> sp., <i>Verrucella aurantia</i>	Rudman 1991
<i>Phyllodesmium serratum</i>	Japan, Australia	<i>Melitodes</i> sp. <i>Clavularia</i> sp. <i>Junceella</i> sp.	Rudman 1991 Sea slug forum
<i>Tritonia festiva</i>	East Pacific	<i>Lophogorgia chilensis</i> <i>Ptilosarcus guernei</i> <i>Alcyonium rudyi</i> <i>Gersemia rubiformis</i> <i>Cryptophyton goddardi</i>	Birkeland 1974 Gomez 1973 Sea Slug Forum

<i>Tochuina tetragueta</i>	North Pacific	<i>Gersemia rubiformis</i> ,	Wicksten and Demartini 1973 Nybakken & McDonald 1981
<i>Armina californica</i>	East Pacific	<i>Renilla koellikeri</i> , <i>Ptilosarcus gurneyi</i>	Bertsh 1968 Birkeland 1974b
<i>Tritoniopsis freydis</i>	Caribbean	<i>Plexaurella sp.</i>	Humann 1992
<i>Tritoniopsis elegans</i>	Hawaii	<i>Carijoa riisei</i> <i>Sarcothelia edmondsoni</i>	Wagner 2009
<i>Okenis mediterranea</i>	Mediterranean Sea	<i>Paramuricea clavata</i>	Cattaneo-Vietti, et al 1990
<i>Aeolidiella glauca</i>	North Sea	<i>Alcyonium digitatum</i>	Walton 1908
<i>Pteraeolidia ianthina</i>	Indo–West Pacific	<i>Sarcothelia edmondsoni</i>	Gosliner 1987
<i>Tritonia Antarctica</i>	Antarctica	<i>Alcyonium paessleri</i>	Barnes 1996

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